

Predicting *Phyllaplysia taylori* (*Anaspidea: Aplysiidae*) presence in Northeastern Pacific estuaries to facilitate grazer community inclusion in eelgrass restoration



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ABSTRACT

Estuarine biodiversity is impacted by climate change and anthropogenic use due to the high productivity of estuarine ecosystems and convenient human use of nearshore areas. Human use of estuaries (e.g. with dredging, filling, and invasive species introductions) has decimated subtidal and marsh ecosystems, thus making them the focus of major restoration efforts. Submerged aquatic vegetation (SAV) such as eelgrass beds, and their associated communities, fall under these restoration efforts, especially in San Francisco Bay. Diverse eelgrass communities that include grazers, such as *Phyllaplysia taylori*, have been shown to maintain eelgrass health and promote increased biodiversity. This study addresses the need for simple, predictive models based on field data for use in SAV restoration that incorporates grazer diversity. Predictive models with ecological, abiotic, and landscape variables were generated that explained the presence of *P. taylori* in eelgrass beds along the coast of the western United States and seasonal patterns in population density. While surprising, the exclusion of abiotic factors in presence/absence model selection suggested that non-point source runoff promotes *P. taylori* populations via increased food and turbidity, resulting in decreased predation. *P. taylori* presence within eelgrass beds was best predicted by the positive impacts of nearshore irrigated land, vegetated land, and bare soil land. *P. taylori* abundance over time within one site was best described by the positive effects of eelgrass density and eelgrass length and the negative effects of epiphytic coverage and average temperature. These models were used to predict habitat suitability for *P. taylori* in seventeen San Francisco Bay eelgrass restoration areas in various phases of completion, indicating a 53% *P. taylori* success rate. Incorporating population persistence knowledge from the SAV-associated invertebrate perspective is a step towards grazer community-minded restoration tactics.

1. Introduction

Estuaries around the world host much of the nearshore marine and terrestrial biological diversity, regulate important biogeochemical processes, and are essential for ports and other water-based industries (Barbier et al., 2011; Carter, 1988). Biological diversity in nearshore estuarine habitats, like seagrasses and mudflats, is often influenced heavily by biotic, environmental, and anthropogenic stressors from terrestrial sources linked to dense coastal human populations and associated industries (Bas Ventín et al., 2015; Coles et al., 2014).. Fluctuations in estuarine biodiversity can reflect species-specific responses to environmental change and perturbations (Blake et al., 2014; Kelly et al., 2016). Of the taxa impacted by environmental change, mollusks have emerged as particularly persistent in population numbers, sometimes even benefitting from anthropogenic inputs to the nearshore

ecosystem (Goddard et al., 2011; Wilson et al., 2016). Kelly et al. (2016) have shown that increases of biological richness in nearshore urbanized estuaries is mainly composed of molluscan taxa. Mollusks are successful invaders via ballast water and other shipping-related transport, so much of this species richness may be comprised of invasive species (Carlton, 1999; Carlton et al., 1990). This does not discount the major successes of native mollusks in estuaries (Coen et al., 2007; Schulte et al., 2009).

Eelgrass beds are a fast-disappearing estuarine habitat due to increased nutrient-rich terrestrial runoff that limits eelgrass photosynthetic scope by increasing epiphytic algal growth, turbidity, and sedimentation (Burkholder et al., 2007; Carr et al., 2011; Orth et al., 2006). Mollusks have the capacity to enhance eelgrass health in a changing climate by filtering the water, and browsing away epiphytic material that inhibits eelgrass blade photosynthesis (Hoellein et al.,

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2015; Thormar et al., 2016; Williams and Ruckelshaus, 1993).

The sea hare, *Phyllaplysia taylori* (Dall, 1900), is a grazer in *Zostera marina* eelgrass beds that feeds on encrusting epiphytes which hinder eelgrass growth by light limitation (Beeman, 1963; Hughes et al., 2010; Lewis and Boyer, 2014). These sea hares have limited dispersal ability, exhibiting direct development and crawl-away young, a life history trait characteristic of many estuarine species (Beeman, 1966). Nevertheless, their reported range is relatively large, from Vancouver B.C. to Baja California, inhabiting both subtidal and intertidal eelgrass beds (Beeman, 1963). There are no records of their strictly intertidal range in the literature, the habitat in which this study was focused. In contrast, the range for *Z. marina* extends from the tropics to the Arctic in both the Pacific and Atlantic Oceans (Short et al., 2010). By surveying habitats categorized as hosting *P. taylori* in historical records, this study examined how modern intertidal populations of *P. taylori* may have been impacted by past and ongoing modifications to their environment, including both abiotic features and shifts in patterns of anthropogenic land use.

This study aimed to identify which ecological, abiotic, and surrounding terrestrial landscape indicators best predict *P. taylori* presence and population density in suitable habitats along the western coast of the United States. Ecological variables characterizing habitat structure and resource availability have long been a focus of marine habitat restoration and protection (Bas Ventín et al., 2015; Burgess et al., 2014; Saarman and Carr, 2013). Landscape features play their largest role as indirect mediators of runoff and nutrient addition to these nearshore habitats (Jiang et al., 2014; Wang et al., 2013). Across taxa, environmental temperature has been shown to be a major driver in population dynamics in all types of intertidal invertebrates (Dahlhoff et al., 2002; Helmuth et al., 2002; Kroeker et al., 2016). As an intertidal species occupying estuarine habitat, *P. taylori* was expected to have high tolerance of predictable fluctuations in both abiotic variables and anthropogenic inputs, but only within the range of conditions currently experienced by a particular population. Estuaries along a latitudinal gradient reflecting multiple environmental profiles may result in populations acclimated to different conditions, thus environmental temperature was expected to explain a significant portion of the variance in *P. taylori* abundance and presence in multiple populations along the western coast of the US.

Using these ecological, abiotic, and surrounding terrestrial landscape indicators, statistical models were generated and tested to predict *P. taylori* presence and abundance over time (at one site) and space (along a latitudinal gradient and within San Francisco Bay). From these developed spatial and temporal models of *P. taylori* presence, existing submerged aquatic vegetation (SAV) restoration sites within San Francisco Bay were evaluated for potential *P. taylori* population persistence. In doing so, this work intended to inform SAV restoration efforts by identifying the key components of the environment that limit population establishment and persistence of one grazer species, *P. taylori* (Boyer and Latta, 2013; San Francisco Bay subtidal habitat goals report, 2010). As a primary consumer of epiphytic material, *P. taylori* plays an important role in limiting the cover of harmful epiphytes within *Z. marina* beds. However, *P. taylori*'s presence likely depends on a complex mix of environmental factors, and not simply food availability (DeLorenzo, 1999; Hughes et al., 2010; Lewis and Boyer, 2014; Williams and Ruckelshaus, 1993). Hughes et al. (2010) found that *P. taylori* in particular increased seagrass biomass due to its complementary nature with genetically diverse polycultures of eelgrass. Multiple studies have shown that top-down control of epiphytes is facilitated primarily by *P. taylori* (Motley, 2017; Shaughnessy et al., 2014). Another study done within Humboldt Bay, CA demonstrated that eelgrass density could be predicted by *P. taylori* abundance (Tennant, 2006). For these reasons, *P. taylori* is a suitable candidate for inclusion in eelgrass restoration efforts and this model takes the first step towards that goal. While *P. taylori* are by no means the only important eelgrass-associated invertebrate (Lewis and Boyer, 2014),

understanding how a grazer species interacts with its environment can inform future community-scale investigations. Determining the relationship between *P. taylori* and its environment is a valuable asset to eelgrass conservation efforts within its geographic range, and as a first-pass model for maintaining grazer species diversity in seagrass restoration. This modeling effort took a simple, robust generalized linear mixed effects approach to maximize predictive power while acknowledging the limitations of field-collected data availability. Four types of models were generated (historical presence/absence, modern presence/absence, high density presence/absence, and temporal) to determine whether *P. taylori* presence was predictable and how this knowledge could be applied towards restoration of this species within San Francisco Bay.

2. Methods

Four datasets were used for parametrizing and testing the model: training, test, predicted, and temporal. Training sites (Table S1) consisted of nineteen field sites along the coast. Test sites (Table S2) consisted of twelve field sites that also had known presence/absence of *P. taylori* with a similar geographic spread as the training data. Seventeen predicted sites were within San Francisco Bay (Table S3) and outlined in the San Francisco Subtidal Habitat Goals Project as ongoing and/or potential restoration sites for eelgrass. The temporal dataset consisted of monthly measurements of ecological and abiotic parameters at one field site, Point Molate, SF Bay, CA starting in November 2015. Four models were generated with these datasets; the first (historical model) attempted to predict records of *P. taylori* in the literature based on present conditions, the second (presence/absence model) evaluated modern presence/absence of the species in a given eelgrass bed, the third (high density presence/absence model) assessed high density (> 30 individuals found in < 1 h) presence/absence, and the fourth (temporal model) estimated *P. taylori* abundance over two years at one field site.

2.1. Ecological measurements in the field

The ecological factors investigated in this study were selected to provide a measure of eelgrass health, relating directly to the substrate and food source of *P. taylori*. To evaluate the relationship between *P. taylori* and its surrounding environment, field measurements of eelgrass health and *P. taylori* abundance were taken at nineteen sites (Fig. 1, Table S1) along the western coast of the United States at one time point during the season of expected *P. taylori* peak biomass, May 2016–September 2016, (Beeman, 1963). To create a temporal model describing *P. taylori* presence through time, eelgrass health and *P. taylori* abundance were monitored once per month at Point Molate in San Francisco Bay, CA for two years (August 2015–July 2017). Eelgrass health was quantified with four measurements: eelgrass frequency, eelgrass density, eelgrass length, and epiphyte abundance along four 30 m transects (standard diver method: Bernstein et al., 2011; San Diego Unified Port District, 1979). These metrics of eelgrass health are strong correlates of eelgrass' secondary productivity (Duffy et al., 2001). Transects were chosen by starting the first transect at the eelgrass bed closest to the shore and running parallel to the shore. Each subsequent transect was placed five meters further from shore. If the eelgrass bed did not extend far enough for four transects to be placed, two transects were placed end to end along the shore instead (i.e., resulting in two 60 m transects). Eelgrass frequency was measured by evaluating the substrate type at every meter on each of the four transects at a site, with each eelgrass measurement counting as one and any other substrate as zero. Eelgrass density was quantified using a 0.25 m² quadrat placed every ten meters on each transect starting with the meter zero mark, where the number of above-ground eelgrass shoots was counted. Eelgrass length was measured within the same 0.25 m² quadrat as an average of all blade lengths within one quadrat (resolution = 5 cm). Epiphyte abundance

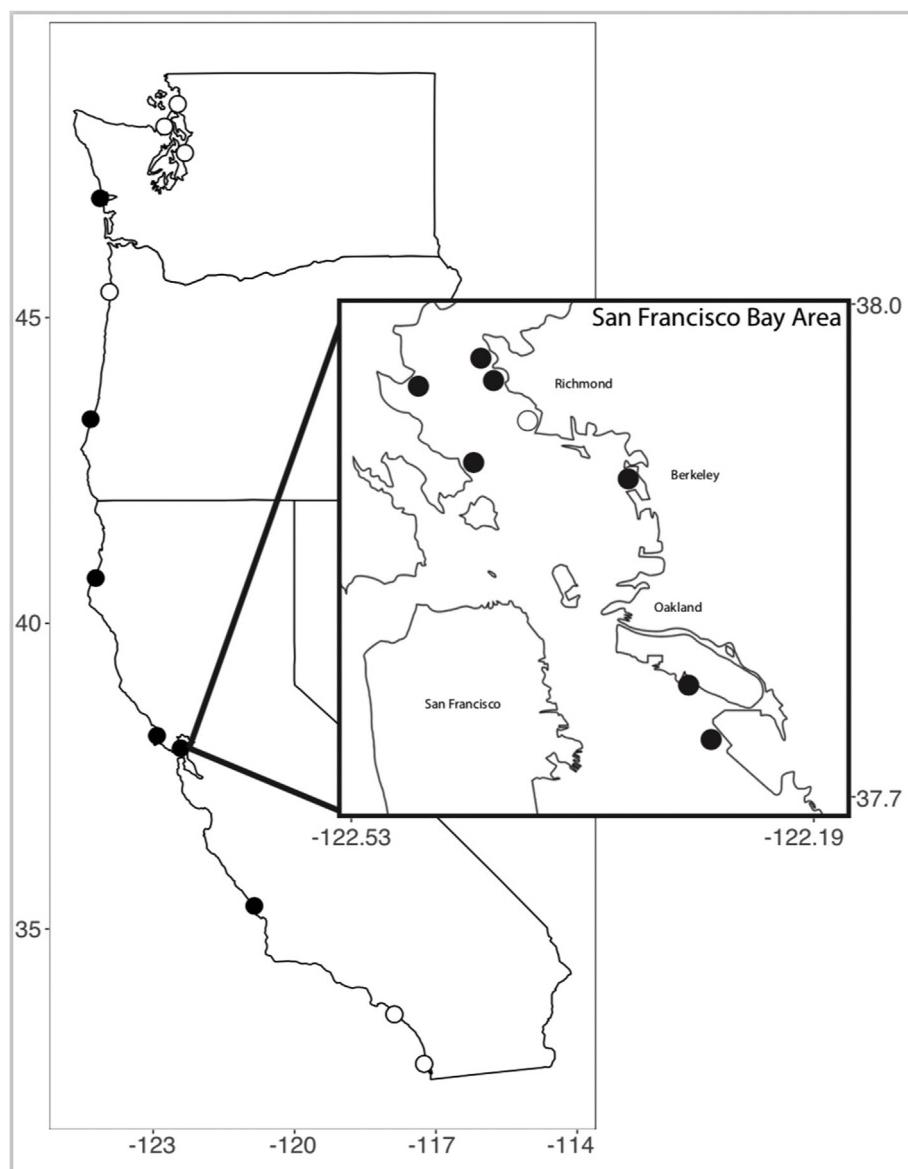


Fig. 1. All locations surveyed for training dataset (see Table S1), where black dots indicate presence and white dots indicate absence of *P. taylori*. The San Francisco Bay Area is enlarged on the right.

was quantified as the percent coverage of all epiphytic growth (encrusting, algal, diatomaceous) on all blades, from stalk to tip, within each quadrat. This was approximated visually by the length of blade covered with brown or red epiphytic growth as a percentage of total blade length in all turions within a quadrat (resolution = 10%). Additionally, *P. taylori* abundance and *P. taylori* average length were measured on above-ground eelgrass shoots originating within the same quadrats (resolution = 0.5 cm).

2.2. *P. taylori* presence/absence

Three measures of presence/absence were obtained at each site: historical, present, and high density (> 30 individuals). Historical records of presence were obtained from the primary literature and resources provided by the online community, iNaturalist (Table S1). All records of absence were documented by the author. If any note of the species (including written or photo) was found before 2015, it was counted as presence. Historical records for this species are lacking, so this may be an incomplete dataset. In each of the field surveys, the presence of any *P. taylori* individual or egg mass was counted as *P.*

taylori presence. To account for spatial heterogeneity in populations within one eelgrass bed, high density presence was recorded during each survey and was designated by > 30 individuals found in < 1 h, or about > 1 individual/2 min of collecting by one researcher (method based on Schultz et al., 2011).

2.3. Abiotic data

The abiotic factors selected for use in this study reflect the importance of *P. taylori*'s thermal physiology in determining population persistence and the influence of water flow on benthic invertebrate population persistence. Due to incomplete records, salinity and dissolved oxygen were not included in this analysis but are acknowledged to be potential major players in the *P. taylori*-environment relationship. For the sites selected in this study, there were no intertidal records of these measurements. Water temperatures collected by weather stations near each field site for January 2015 through December 2015 were downloaded from the National Data Buoy Center and the National Estuarine Research Reserve (Table S4). If data were not available in the bay of the field site, the closest bay with similar physical structure and

station placement was chosen. Data were summarized by 2015 average temperature and 2015 average daily variation (range between maximum and minimum temperature each day averaged over all days) (Fig. S1). At Point Molate, temperature was recorded at 30-min intervals at two tidal heights using Maxim Integrated® iButton® thermochron loggers (San Jose, CA, USA) and Onset® UTBI-001 Tidbit® v2 loggers (Bourne, MA, USA) starting in November 2015. These data were used for the temporal model only. Data were summarized by monthly average temperature and monthly average daily variation.

Other geographical features at each field site were evaluated using Google Earth 7.3.0.3832 (64-bit), which included linear distance from the mouth of the estuary (i.e., where it meets the outer coast) to the midpoint of the transects and a categorical assessment of protection. The level of protection from currents was evaluated categorically, with 0 directly exposed to oceanic or estuary channel currents, 1 being within a small cove or lagoon, and 2 being directly behind the point of a small cove or lagoon (i.e. behind a jetty) (Fig. S2).

2.4. Land use satellite imagery

Landscape variables were incorporated into this study to reflect the importance of urbanization in shaping nearshore environments. Satellite imagery was downloaded from Google Earth 7.3.0.3832 (64-bit). Extent and type of urbanization was categorized using a 500 × 500 m grid overlay using ImageJ 1.49v (Schneider, 2012) on the 500 m of adjacent coastline of each field site extending 500 m inland. This 500 × 500 m square was centered on the Global Positioning System (GPS) coordinates (Table S1) of the first transect for each site, with the ocean side of the square aligning with the coastline as closely as possible. Selection of landscape bins was based on methods for detecting the urban heat island effect (Kalnay and Cai, 2003), most importantly including measures of water-impervious structure areas, vegetated areas (including both woody and grassy vegetation types), bare soil areas, and irrigated land. Categories included irrigated land, > 50% water-impervious structures (primarily concrete, hereafter referred to by concrete) cover, < 50% concrete cover, bare soil, and vegetated. Imagery was evaluated during wet seasons to account for full potential vegetation coverage. Each grid square was evaluated for the above criteria and percent cover of each land use type was totaled for each field site.

2.5. Statistical analyses

All candidate models tested were created using a generalized linear mixed effects ANOVA with one random effect. For a list of all parameters included in the full model, see Table S5. All metrics were centered so that the predictors have a mean of zero. Candidate generalized linear models were generated based on known ecological relationships, effects of water flow on population persistence, and assumed correlations between land use and runoff generation (Ongsomwang and Pimjai, 2015; Paule et al., 2014). All metrics were first evaluated for possible interactions. The two measures of concrete or building cover had high collinearity and an inverse relationship, thus only > 50% concrete or building cover was used in generating models. Using R v. 3.1.1 (R Team Core, 2017) with packages “MuMin”, “lme4”, “lmerTest”, “nlme”, and “effects”, generalized linear mixed effects models with one random factor for field site were generated for the presence/absence models, high density models, and historical data models. To test for a relationship between *P. taylori* and the environment over time, linear mixed effects models were generated with transect number and quadrat number as random effects and a time (month, year) autocorrelation structure established for transect number and quadrat number. Landscape variables were not used in the temporal model due to their static nature in considering only one site on a short timescale. Models were then compared using the Akaike Information Criterion (AIC) with correction for small sample sizes relative

to number of explanatory variables (AICc) using the “AICmodavg” package. Models with $\Delta\text{AICc} > 2$ were rejected as poor relative fit, as $\Delta\text{AICc} < 2$ is the accepted cutoff for choosing the model with the most predictive power (Compton et al., 2002).

Presence/absence (binomial) models were generated with training data with three response variable options: historical presence of *P. taylori* at each site as found in the primary literature and educational/citizen science networks, presence of *P. taylori* at each site in 2016 during surveying, and high-density presence of *P. taylori* at each site in 2016 during surveying (Table S1). Models were validated using the test dataset (Table S2) and later applied to restoration sites in San Francisco Bay (Table S3) using the “predict” function and the appropriate fit from the training data. Temporal models were generated accounting for temporal autocorrelation, a nested study design, and assumed unequal variances between collection dates.

3. Results

3.1. Predictive model selection: presence/absence

Phyllaplysia taylori presence within eelgrass beds at time of collection (2016) was best predicted by the positive impacts of irrigated land percentage, bare soil percentage, and vegetation percentage with a random effect for location (Tables 1 and 2, $\Delta\text{AICc} = 0$). Bare soil had about twice the positive effect of either of the other two predictors (see Table 1). No ecological or abiotic factors were selected in the best fit model. All models attempting to predict *P. taylori* historical presence using all available parameters did not converge except one containing irrigated land percentage, bare soil percentage, and vegetation percentage, in which only irrigated land percentage was significant ($p < 0.05$). An AICc could not be run with one converged model in which only one parameter was significant in only that configuration of parameters. *Phyllaplysia taylori* high density presence was best predicted by the positive impacts of the level of protection, average temperature, and bare soil percentage and the negative impacts of average daily variation (Tables 3 and 4, Fig. S3, $\Delta\text{AICc} = 0$). The positive effects of protection had the highest relative weight in the model, followed by the positive effects of average temperature. The positive effects of bare soil and average daily variation each had half the weight of these variables, with average daily variation having the only negative impacts (see Table 3). High density *P. taylori* presence was also well-explained by the same parameters minus bare soil percentage (Tables 3 and 4, $\Delta\text{AICc} = 0.84$). In this model, all three variables held similar importance, with the same directionality of impacts (see Table 3).

3.2. Presence/absence model testing and application: restoration insights

The most basic presence/absence best fit model was selected for application to restoration areas because of the limited availability of test dataset parameters. Five sites with confirmed *P. taylori* presence in the year preceding the study (starting May 2015) and seven sites with confirmed *P. taylori* absence during the study were used to test the selected model (Table S2). Data were collected from these sites in the same manner as for the model itself, however, only landscape variables were obtained due to the exclusion of ecological and abiotic variables

Table 1

Results from the generalized linear mixed effects model of *P. taylori* presence predicted by irrigated land coverage, bare soil coverage, and vegetated land coverage with a random effect for location.

Fixed Effects	Estimate	Standard Error	df	z value	Pr (> z)
Generalized linear mixed effects model (AIC = 17.7)					
Irrigated Land	37.584	8.170	1	4.900	4.22e-06
Bare Soil	58.297	9.069	1	6.428	1.29e-10
Vegetated Land	32.088	7.323	1	4.382	1.18e-05

Table 2AICc results for all candidate models for predicting *P. taylori* presence.

Model fixed effects	K	AICc	ΔAICc	Akaike Weight	Cumulative Akaike Weight	Log likelihood
Irrigated Land, Bare Soil, Vegetated Land	5	17.8980	0.0000	0.5321	0.5321	-3.8434
Vegetated Land, Bare Soil	4	20.2601	2.3621	0.1633	0.6954	-6.0598
Concrete over 50%, Bare Soil, Vegetated Land	5	20.7868	2.8889	0.1255	0.8209	-5.2878
Average Daily Variation, Average Temperature, Concrete over 50%	5	20.8720	2.9740	0.1203	0.9412	-5.3303
Protection, Average Temperature, Average Daily Variation	5	25.2469	7.3489	0.0135	0.9547	-7.5178
Bare Soil	3	26.0181	8.1201	0.0092	0.9638	-9.9671
Protection	3	26.0379	8.1399	0.0091	0.9729	-9.9770
Irrigated Land	3	26.1366	8.2386	0.0086	0.9816	-10.0263
Average Temperature	3	26.1433	8.2453	0.0086	0.9902	-10.0297
Concrete over 50%	3	26.1447	8.2468	0.0086	0.9988	-10.0304
Eelgrass Frequency, Epiphyte Coverage, Concrete over 50%, Bare Soil	6	30.1037	12.2058	0.0012	1.0000	-8.9035

Table 3Results from the generalized linear mixed effects model of *P. taylori* high density presence. Two accepted candidate models are shown below, both including the factors of level of protection, average temperature, and daily variation in temperature, and one including bare soil as well.

Fixed Effects	Estimate	Standard Error	df	z value	Pr (> z)
Generalized linear mixed effects model (AIC=23.4)					
Protection	230.559	1.508	1	152.94	< 2e-16
Average Temperature	195.051	1.441	1	135.39	< 2e-16
Average Daily Variation	-52.281	1.798	1	-29.08	< 2e-16
Bare Soil	60.653	2.007	1	30.23	< 2e-16
Generalized linear mixed effects model (AIC=24.3)					
Protection	63.742	2.876	1	22.162	< 2e-16
Average Temperature	58.577	3.939	1	14.871	< 2e-16
Average Daily Variation	-43.368	3.143	1	-13.796	< 2e-16

from the selected best fit model (Fig. S4). Out of the five presence sites, four were validated by the model (80% success) and out of the seven absence sites, five were validated by the model (71.4% success) (Fig. 2). Seventeen sites in all phases of SAV eelgrass restoration in San Francisco Bay were evaluated using the model (Fig. S5) and eight sites were indicated as having potential *P. taylori* presence. Out of these sites, seven were in Phase I and one was in Phase II & III. Two sites, Corte Madera Bay and San Rafael Bay, overlapped between Phase II and III. Therefore, 50% (7/14) of Phase I sites had potential *P. taylori* presence, 50% (1/2) of Phase II sites, and 33% (1/3) of Phase III sites had potential *P. taylori* presence. Of the Phase I sites in the small-scale test plot phase (I-3), 43% (3/7) were designated as having potential *P. taylori* presence. Overall, 53% of active SAV eelgrass restoration sites are predicted to be habitable for *P. taylori* (Fig. 3). While environmental conditions are known to vary based on latitude within SF Bay due to large differences in environmental factors (temperature, salinity, flow rate) (Schraga and Cloern, 2017), no bias in location (north vs. south bay) was found, with two presence indications in the north bay, three in the mid-bay, and three in the south bay.

Table 4AICc results for all candidate models for predicted high density *P. taylori* presence.

Model fixed effects	K	AICc	ΔAICc	Akaike Weight	Cumulative Akaike Weight	Log likelihood
Protection, Average Temperature, Average Daily Variation, Bare Soil	6	23.6788	0.0000	0.3701	0.3701	-5.6910
Protection, Average Temperature, Average Daily Variation	5	24.5151	0.8363	0.2436	0.6137	-7.1519
Protection	3	26.0074	2.3286	0.1155	0.7293	-9.9617
Average Temperature, Bare Soil	5	26.1981	2.5193	0.1050	0.8343	-9.0289
Average Temperature, Average Daily Variation, Bare Soil	5	27.6951	4.0162	0.0497	0.8840	-8.7419
Bare Soil	3	28.1229	4.4440	0.0401	0.9241	-11.0195
Protection, Bare Soil	4	28.1316	4.4527	0.0399	0.9640	-9.9956
Vegetated Land, Bare Soil	4	29.8465	6.1676	0.0169	0.9810	-10.8531
Concrete over 50%, Bare Soil, Vegetated Land	5	31.7052	8.0264	0.0067	0.9877	-10.7470
Irrigated Land, Bare Soil, Vegetated Land	5	31.8853	8.2064	0.0061	0.9938	-10.8370
Average Temperature	3	32.5984	8.9195	0.0043	0.9981	-13.2572
Eelgrass Frequency, Epiphyte Coverage, Concrete over 50%, Bare Soil	6	34.1732	10.4944	0.0019	1.0000	-10.9382

3.3. Predictive model selection: *P. taylori* abundance on a temporal scale

Phyllaplysia taylori abundance over time was best explained by a linear mixed effects model containing the positive effects of eelgrass density and eelgrass length and the negative effects of epiphytic coverage and average environmental temperature (Tables 5 and 6 Fig. S6, $\Delta\text{AICc} = 0$). Eelgrass length and average temperature had the strongest relative effects in the model, with epiphytic coverage and average temperature having negative effects and eelgrass length and eelgrass density having positive effects (see Table 5). No models had significant collinearity among parameters. While the above model was selected for best predicting *P. taylori* presence, the fit resulted in a high residual variance (sum of squares residuals = 211.7) despite individual factors being significantly correlated with the response variable.

4. Discussion

Phyllaplysia taylori population structure was expected to fluctuate with shifts in its environment, including all measured ecological, abiotic, and landscape indicators. Surprisingly, results showed that presence is most dependent on landscape variables, while high-density populations can be predicted by temperature trends in addition to these landscape variables. Population density over time is dependent on ecological variables, i.e. eelgrass health metrics. These models may differ in their scope of included variables due to *P. taylori* life history traits, namely limited dispersal and direct development. While low density populations may face barriers to growth due to Allee effects, high density populations face more complex challenges to population persistence with limitations on food, impacts of predation, and maintaining genetic diversity (Chambers, 1934; Dennis, 1989).

4.1. *P. taylori* presence model

It was surprising that of the factors considered, landscape factors best explained where *P. taylori* were found. This indicates that most

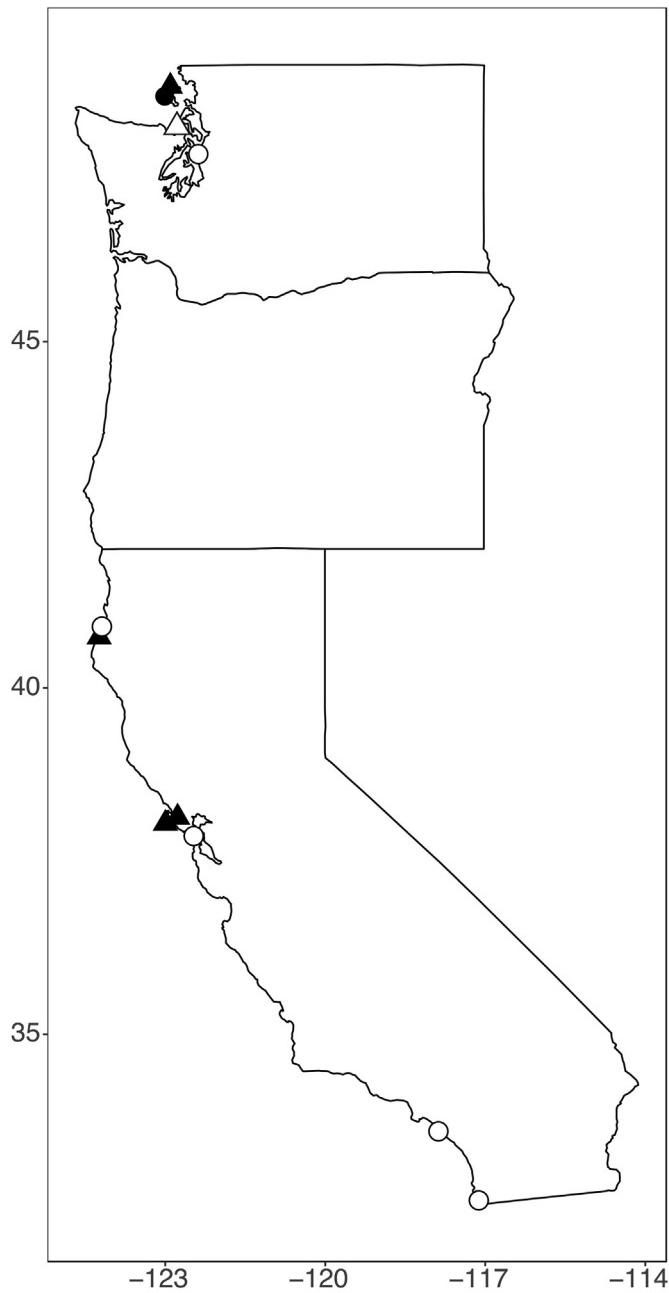


Fig. 2. Test dataset results (see Table S2), where shapes indicate *P. taylori* presence as predicted by the model (triangle = present, circle = absent). Fill indicates observed *P. taylori* presence (filled = present, open = absent). Model and observation convergence results in filled triangles and open circles.

likely localized terrestrial runoff, not ocean processes, promotes the presence of this sea hare. Since landscape factors did not necessarily correlate with the amount of human interaction with nearshore environments, there is not a consistent correlation with boat traffic, light pollution, or any other anthropogenic interference with nearshore eelgrass beds. Small-scale point sources of terrestrial runoff could promote *P. taylori* presence for many reasons, but two distinct possibilities are (1) runoff contains additional nutrients that promote epiphyte growth and therefore *P. taylori* population growth (Burkholder et al., 2007), and (2) runoff increases turbidity resulting in decreased predation on *P. taylori* individuals (Fabricius, 2005; James and Heck, 1994).

Extra nutrients from runoff are known to cause eutrophication in some ecosystems (Burkholder et al., 2007) and provide additional elements that are typically limiting in an ecosystem. Eelgrass beds with an

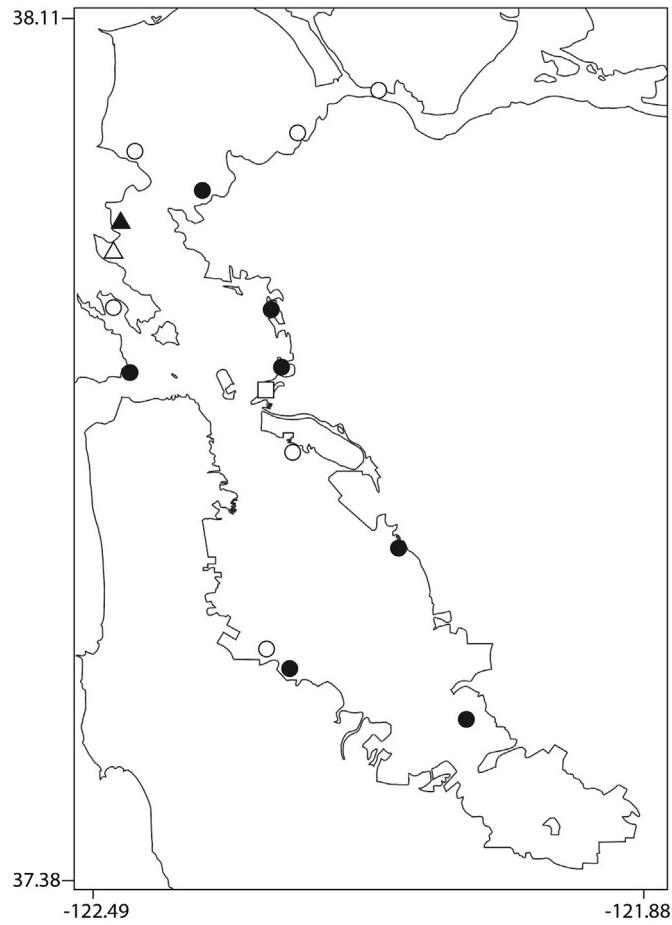


Fig. 3. Predicted dataset results. Shapes indicate restoration phase of SAV restoration areas as noted in the San Francisco Bay Subtidal Habitat Goals Project (see Table S3) (circle = Phase I, triangle = Phase II, square = Phase III). The two sites in Phase II are also listed as being part of Phase III, but are represented only by triangles. Fill corresponds to predicted *P. taylori* presence (filled = present, open = absent).

Table 5

Results from the linear mixed effects model of trends in *P. taylori* abundance over time.

Fixed Effects	Estimate	Standard Error	df	t value	p value
Linear mixed effects model (AIC = 593.14)					
Eelgrass Length	0.467	0.083	178	5.643	0.0000
Eelgrass Density	0.218	0.078	178	2.786	0.0059
Epiphyte coverage	-0.178	0.080	178	-2.224	0.0274
Average Temperature	-0.425	0.076	178	-5.564	0.0000

influx of nutrients typically have higher rates of epiphyte growth, especially of the algal variety (Nelson, 2017; Williams and Ruckelshaus, 1993). Since *P. taylori* rely on these epiphytes for food, population growth could be exponential if epiphyte growth rates remained high due to increased runoff. Even though eelgrass growth is not nutrient-limited in San Francisco Bay (Santos, 2013), the threshold for nutrient limitation in food quality for sea hares may be higher, and therefore influenced more heavily by runoff. Since *P. taylori* feed unselectively, a shift in epiphyte composition, or an increase in higher nutrient food, may benefit growing populations.

In addition to the extra nutrient influx resulting from runoff, *P. taylori* may benefit from increased turbidity. *Phyllaplysia taylori* have lower chemical defenses when compared with sea hares like *Aplysia californica*, meaning they rely on other methods of predator avoidance (Takagi et al., 2010). In predator-prey relationships (i.e. seahorse-

Table 6AICc results for all candidate models for predicting temporal trends in *P. taylori* abundance.

Model fixed effects	K	AICc	ΔAICc	Akaike Weight	Cumulative Akaike Weight	Log likelihood
Eelgrass Length, Eelgrass Density, Epiphyte Coverage, Average Temperature	9	594.1006	0.0000	0.8033	0.8033	-287.5716
Eelgrass Length, Eelgrass Density, Average Temperature	8	596.9144	2.8138	0.1967	1.0000	-290.0762
Eelgrass Length, Eelgrass Density	7	621.7953	27.6948	0.0000	1.0000	-303.6029
Eelgrass Length	6	630.6019	36.5013	0.0000	1.0000	-309.0811
Average Temperature	6	630.8019	36.7014	0.0000	1.0000	-309.1811
Eelgrass Density	6	634.5862	40.4857	0.0000	1.0000	-311.0732
Eelgrass Frequency	6	638.9047	44.8041	0.0000	1.0000	-313.2324

shrimp), increased turbidity and light limitation increased predator evasion, while increased seagrass structure had a negligible effect (Jackson et al., 2001; James and Heck, 1994). Therefore, it is possible that there are multiple ways that runoff can enhance *P. taylori* populations: increases in food quality and predator evasion opportunities.

While locations with *P. taylori* represent a wide variety of landscape conditions, those without *P. taylori* are more limited in scope of predictor variables. Although land characteristics immediately surrounding an intertidal eelgrass bed may be positively correlated with *P. taylori* presence, this study acknowledges the shortcomings of assuming high impacts of small-scale terrestrial runoff. Future studies should investigate point sources of storm drain runoff, as many field sites included in this study corresponded with direct pipe outflow. Analyses of water content in these outflows would shed light on whether they positively contribute to eutrophication in the same way that purely land-based runoff does. Additionally, it is necessary to confirm the hypothesis that extra nutrients translate to higher quality food for *P. taylori* by shifting epiphyte community composition.

4.2. *P. taylori* high-density model

As anticipated, the high-density presence/absence model built upon the basic presence/absence model, but also incorporated the level of protection from wave action and temperature effects. This model included the most types of indicator parameters, highlighting the complexity of a grazer's interactions with the environment. Average temperature and average daily variation in temperature showed opposing correlations with *P. taylori* high density, which demonstrated that areas with high average temperature had little fluctuation and vice versa. This relationship mimics a global pattern between the tropic and temperate zones, resulting in narrower tolerance windows in locales with higher averages and lower daily variation, per the Climate Variability Hypothesis (Compton et al., 2007; Pörtner, 2002; Stevens, 1989). Multiple studies have demonstrated a trade-off in physiological plasticity for marine populations exposed to high temperature versus high fluctuations in temperature, which could mean this species may exhibit thermal tolerance physiological traits typical of the Trade-Off Hypothesis (Gunderson and Stillman, 2015; Pörtner, 2012; Stillman, 2003). This could explain why a high-density population is closely tied to temperature, as it may be a driver of key traits that determine fitness (Addo-Bediako et al., 2000; Angilletta et al., 2003; Gibson et al., 2011; Magozzi and Calosi, 2015; Stillman, 2002). Bare soil as an indicator landscape parameter carried over from the presence/absence model, which is indicative of the high level of nutrient runoff associated with it. The level of protection from currents as a parameter included in the model was not a primary candidate initially, but it is plausible that protection from currents would prevent existing *P. taylori* from washing away and allow for population growth. The findings from this specific model supported those of the presence/absence model, but did not build substantially upon them. The results from this model would be strengthened by further investigations of variation in *P. taylori* phenotypes across populations, especially in relation to thermal tolerance.

4.3. Temporal *P. taylori* abundance model

The combination of a temporal and spatial approach in this study provides perspective on not only where to find *P. taylori*, but how populations are sustained. Interestingly while presence/absence models relied heavily on land use parameters, eelgrass structure (e.g. length, density, frequency of shoots) can successfully predict seasonal patterns in *P. taylori* biomass. Therefore, it is important to first select habitats in line with the presence/absence model predictions when using *P. taylori* in eelgrass restoration but also maintain eelgrass beds that provide structure and food to aid in *P. taylori* population establishment and persistence. Since *P. taylori* contribute positively to eelgrass health by clearing epiphytic growth from blades, current restoration efforts may benefit from including this macroinvertebrate with initial eelgrass planting instead of later introduction to reduce the amount of restoration effort required for maintaining eelgrass beds. Additionally, the temporal model indicates that *P. taylori* depend on seasonal shifts in eelgrass structure, which will become more pronounced with bed establishment.

Average monthly temperature at Point Molate, SF Bay, CA followed a predictable seasonal pattern with warming in the summer and cooling in the winter. It was unexpected that daily variation did not covary with average temperature or indicate *P. taylori* abundance, as summer conditions coincided with low variability and winter conditions were characterized by high variability in daily temperatures. However, the Point Molate population of *P. taylori*, among many other populations, experiences two generations per year with peaks in maturity during the mid-summer and spring, resulting in peak biomass expressed during the following asymmetrical thermal regimes (Beeman, 1966). Therefore, average temperature during *P. taylori* maturity for either generation, not daily variation, best explains *P. taylori* abundance, since average temperature at this temperate latitude during the summer and spring are within a few degrees of each other. Peak biomass falls within seasons with different thermal regimes, but the most thermally sensitive life stages are during development, or close to peak maturity (Gibson et al., 2011). Therefore, the potential for peak biomass is not set by the temperature conditions in which it is expressed, but instead by the immediate thermal history.

4.4. A model biased by life history characteristics: the potential role of limited dispersal

Despite a survey of over a dozen parameters from three diverse sources (abiotic, ecological, and landscape), linear models selected as best fit by the AICc had high residual variance. There are limitations to using linear mixed models, some of which include overestimation of effect size and inflation of Type I error rate (Schielzeth and Forstmeier, 2008). By these principles, it would be expected that these models should actually present low, not high, relative residual variance when compared with other methods. Consequently, there may be a biological reason for high residual variance in the best fit model: extremely limited dispersal due to direct development in offspring and no swimming mechanism in adults is predicted to lead to high outbreeding depression and reduced connectivity between populations even in close spatial

proximity to each other. Therefore, it is possible that the establishment of *P. taylori* populations is most dependent on chance events caused by shifts in flow regimes or ship traffic. This study provides clear evidence for the need to investigate the population genetics of this species across the latitudinal and local spatial scales. Based on the results of this study, chance events of population establishment and no patterns in population relatedness on a spatial gradient are expected.

Other environmental factors including salinity, O₂ concentration, pH, and nutrient levels were not considered in this study due to field equipment constraints. These data are freely available in some locales, namely within San Francisco Bay, provided by the USGS. However, the spatial resolution of these measurements is limited to mid-channel cruises (Schraga and Cloern, 2017). Salinity gradients within estuaries are highly dependent on topography, and differ based on freshwater inputs, depth, and flow rate (Monismith et al., 2002; Telesh and Khlebovich, 2010). Therefore, even though some bays surveyed had available salinity measurements from deep channel waters, localized processes for intertidal eelgrass beds were considered to have little relation to more stable measurements from mid-channel (Walters et al., 1985). Inclusion of these abiotic parameters would have strengthened the presence/absence models, as estuarine systems fluctuate heavily in these factors on daily through yearly time scales. For these measurements to be useful, they would have to reflect more similar conditions to local eelgrass beds than the data currently available do. However, for the models predicting *P. taylori* populations over relatively short, seasonal temporal scales, the inclusion of these factors may have had a negligible effect. Ocean acidification in particular has a surprisingly negligible effect on sea hares, where lower average pH resulted in slightly higher *P. taylori* biomass (Hughes et al., 2018). A study by Smart et al. (2012) found little influence of many of these environmental indicators on reproductive phenology in estuarine polychaetes. The high amplitude and frequency of fluctuations in these abiotic parameters may be responsible for the evolution of extreme tolerance in estuarine animals, resulting in little predictive power of a population's growth (Elliott and Whitfield, 2011). When considering population establishment of *P. taylori*, abiotic fluctuations may play a larger role.

In particular, salinity can be a major driver of invertebrate communities in estuaries. Lower salinity exposure in the laboratory resulted in decreased survival in three species of crustaceans, and *P. taylori* themselves have an apparent salinity threshold of 24 psu in summer populations (Faye, 2017; Sur, 2016). However, *P. taylori* have been recorded in the wild at salinities as low as 8 psu in winter months (Beeman, 1963, R. Tanner unpublished data). Salinity is a seasonally-dependent driver of population success in *P. taylori*, with generational timing resulting in peak population biomass in seasons that differ in salinity regimes (Beeman, 1963; Faye, 2017). For this reason, average salinity over long time periods is not likely to contribute significantly to a model of *P. taylori* abundance and fine-scale measurements (i.e. hourly to daily) in intertidal eelgrass beds are most relevant to population persistence in *P. taylori*.

More work needs to be done on how *P. taylori* is able to disperse and establish new populations. Within-bay estimations of dispersal can be accomplished using hydrodynamic models incorporating flow, salinity, and temperature, but latitudinal-scale dispersal is best informed by a survey of population genetics. Previous observations by field biologists have indicated many possible phenotypes of *P. taylori*, which is indicative of high levels of isolation between populations (Beeman, 1963).

4.5. *P. taylori* population persistence and expansion in the face of climate change

All ecological, landscape, and abiotic factors included in all models are influenced by climate change and anthropogenic activities. As the eelgrass substrate, *Z. marina*, is a widespread species, shifts in mean temperature with expected anthropogenic CO₂ inputs to the

atmosphere are not expected to negatively impact the species. In fact, increased growth is expected with warming (Thom et al., 2014). If eelgrass growth is not outpaced by epiphytic algal growth, ecological factors measured in this study will not be negatively impacted. Epiphytic growth, however, is influenced by a myriad of factors including temperature, nutrients, and flow (Williams and Ruckelshaus, 1993). It is unclear how climate change will impact epiphytic growth specifically, but it is generally accepted that it will increase with warming (Howard and Short, 1986). Land use and runoff rates will also change as coastal cities become more crowded and adequate land for agriculture will become sparse. The temperate climate of coastal shores makes them highly desirable for many human uses, so it is reasonable to expect significant coastal land use changes in watersheds feeding eelgrass beds. Additionally, nearshore use – both with increasing infill and/or boat traffic – could play a large role in the existence of these eelgrass beds. All of these changes make a future for *P. taylori* populations uncertain; however, even with current levels of anthropogenic impacts on the climate and land and water use, *P. taylori* still persist at their current population abundance, barring extreme weather events. From this study, the effects of climate change are expected to act on a population-specific level, furthering the genetic and physiological divergence expected in existing populations. While some populations may flourish, others may face local extirpation. The predictive power of the models created here is not great enough to determine future impacts at the population level. Another thing to consider is the episodic nature of this sea hare species in San Francisco Bay, documented by Kathryn Boyer (personal communication, San Francisco State University) and the author. Since it is unclear why populations are ephemeral and the geographic extent of this phenomenon, it could mean that the models described here are valid under an environmental regime that has not undergone catastrophic events, like flooding. These extreme events have the potential to further bottleneck populations and reduce available genetic variation to withstand future climatic shifts.

5. Conclusion

The role of *P. taylori* as an epiphyte grazer in eelgrass beds may be important to habitat restoration efforts, but forecasting where sea hare populations will be established and how they are maintained depends on a number of abiotic, ecological, and landscape parameters at different temporal resolutions. Anthropogenic land use plays a large part in promoting *P. taylori* presence, whether that is because of increased nutrients facilitating epiphytic growth or increased turbidity aiding predator evasion. Surprisingly, ecological characteristics of habitat structure and resources were least important in a survey of *P. taylori* presence at high and low densities. Limited dispersal in *P. taylori* introduces potential bias for models presented here, especially with random population establishment and resulting genetic drift or divergent selection between sites. This study provides a foundation for future modeling efforts investigating how estuarine invertebrates respond to many environmental factors and what this can mean for restoration efforts. It demonstrated how a model based on a fairly limited amount of field data can still predict certain aspects of community composition, which could prove useful in other remote areas or with rarely seen species. Future models should include additional abiotic factors, especially when considering the impacts on organismal physiology. In predicting the presence of *P. taylori*, this study makes a necessary step towards successful incorporation of grazer community diversity into eelgrass restoration efforts.

Conflicts of interest

The author declares no competing interests.

Data accessibility

Data is available at SEANOE (<http://www.seanoe.org>) under reference number 56730.

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Appendix A. Supplementary data

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